caused strong chemical action, sparks and flashes of light, the formation of a colourless salt, and prevented the blue colour, and finally produced a violent detonation, by which the whole of the tube was shattered to small particles. Anhydrous carbonate of sodium caused the blue colour first produced to gradually disappear; the residue was quite colourless, and entirely soluble in water. Anhydrous formiate of soda produced similar effects. Crystals of oxalate of ammonia produced chemical action, destroyed the blue colour first produced, and left a colourless residue which contained no free carbon. Sesquioxide of chromium did not prevent the blue colour, nor show any signs of reduction or other chemical change. Sesquioxide of uranium prevented the permanency of the blue colour.

I have not specially classified the results of these experiments, but may remark that the only elementary substances soluble in anhydrous ammonia are the alkali metals proper, also iodine (bromine was not tried), sulphur, and phosphorus. The more commonly soluble inorganic salts are nitrates, chlorides, bromides, and iodides; whilst oxides, fluorides, carbonates, sulphides, and sulphates were very generally insoluble. Many saline substances, especially certain chlorides, bromides, iodides, and sulphates, absorbed ammonia copiously, and swelled greatly, but did not dissolve. The behaviour of the chlorides of mercury was peculiar.

In many of these experiments chemical changes took place, and new products were formed; but I did not analyze those products, because that was not my object: these chemical reactions offer a field for future investigators. The sulphides of antimony and cadmium, and the sulphates of mercury and manganese, imparted a purple tint to the liquid; sulphur behaved similarly.

February 6, 1873.

Sir GEORGE BIDDELL AIRY, K.C.B., President, in the Chair.

The Right Hon. Hugh Culling Eardley Childers was admitted into the Society.

The following communications were read :—

I. "On the Osteology of the *Hyopotamidæ*." By Dr. W. Kowalevsky. Communicated by Prof. Huxley, Sec. R.S. Received December 19, 1872.

(Abstract.)

The paper laid before the Society is intended to fill a certain deficiency in our knowledge of the extinct creation by giving a complete osteology of a family of Paridigitate Ungulata, which, by the completeness of its skeleton, unreduced number of digits, and rich development in generic

and specific forms, I deem to be of great importance in our speculations on the pedigree of living Ungulata Paridigitata.

On theoretical grounds, as well as from the consideration of rudimental parts in living Paridigitata, anatomists have always supposed that fossil representatives of this family, which could be regarded as the progenitors of the recent Paridigitata, would certainly exhibit a much less reduced skeleton and a more complete number of digits than the recent genera do. Yet, strange to say, such complete forms were not forthcoming, and, if assumed on the evidence of their teeth, very little was known about the structure of their bony frame. My statement will sound like an exaggeration; but still it is true, that since the time of Cuvier, who shortly noticed the tetradactyle *Dichobune*, and Blainville, who gave a very imperfect description of *Cainotherium*, we have absolutely not a single paper in which the osteology of an extinct genus of Paridigitata has been fully given *. This may partly be the reason that the pedigree of living genera has hitherto been so obscure.

The Paridigitata of the Paris gypsum, described in a masterly way by Cuvier (the *Anoplotherium* and *Xiphodon*), were clearly extremely reduced descendants of some earlier more complete forms; their feet presented, in fact, nearly the same degree of reduction which we find in our recent Ruminantia, save the confluence in a cannonbone. Seeing the reduced state of their skeleton, how could they be taken as progenitors of the very rich family of Ruminants, some of which have retained, even till our times, a tetradactyle limb? However, so great was the want of some form from which the living Ruminantia could be assumed to be derived, that nearly all comparative anatomists and palæontologists who speculated on these questions of descent, placed the *Anoplotherium* and *Xiphodon* at the head of the series, as the *fons et origo* wherefrom all living Ruminantia have descended.

The present paper is an attempt to introduce to palæontologists a new form, which, though known by its dental system more than twenty-five years ago, has remained totally unknown, so far as its skeleton is concerned. This skeleton, by its completeness, has proved to be a very interesting one, not only in a concrete way, but as furnishing a clue to the understanding of the skeletons of those forms which, though totally unknown, must have preceded *Anoplotherium* and *Xiphodon* in time, and from which these two may have descended.

Besides, the greater importance of the *Hyopotamidæ* in comparison with *Anoplotherium* and *Xiphodon* lies in the fact, that, while these two last were but poorly differentiated, presenting only two or three distinct specific forms, the *Hyopotamidæ*, on the contrary, strike us by the extreme diversity and richness of their specific and generic forms. Beginning

* No doubt we have excellent memoirs, like the works of Gaudry, Rutimeyer, Fraas, and H. v. Meyer; but the Paridigitata described in all these do not materially differ from those now living, at least so far as the skeleton is concerned.

in the Middle or Lower Eocene of Mauremont, they existed until the Lower Miocene period; and judging by the great number of species and genera, they must have filled in the fauna of this period the same important place which the greatly diversified Ruminantia fill in the fauna of our own times. Indeed the differentiation of *Hyopotamidæ* may be said to be even greater, in point of size, as they range from the *Hyopotamus Renevieri*, not larger than a rabbit, to the great *Anthracotherium* of Rochette, which is as big as our Hippopotamus—all the intermediate stages between these two extremes being represented by different genera, subgenera, and species of the same family.

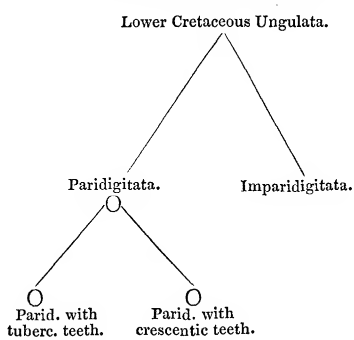
I hope that the rich development of this much neglected family will arouse the attention of palæontologists, and that the skeletons of the different members will be more thoroughly investigated. For my own part, though fully convinced that many of the Eocene *Hyopotamidæ* from Mauremont and Egerkingen present, even in their teeth, characters enough to separate them into distinct genera, I shall not do this, as the multiplication of fossil genera, founded solely on dental characters, without adequate knowledge of the skeleton, is more an obstruction than a help to the progress of palæontology.

This refers to the Eocene *Hyopotamidæ* of Mauremont and Egerkingen; for having found that among the Eocene members of this family there is one which has lost its lateral digits and acquired a didactyle foot, very like an *Anoplotherium*, I was obliged to separate this reduced form from its tetradactyle congeners under the name of *Diplopus* (double foot), while the tetradactyle species of the same family will form the genus *Hyopotamus*. This diversity among the representatives of the same family is very interesting; something of the same kind is, however, to be found in our own times in the *Hyomoschus*, subsisting side by side with the more reduced ruminants, though this is not an entirely parallel case. Moreover, as we have in the *Hyopotamidæ*, so to say, father and son existing together (the complete form together with the reduced), and as, besides, this son bears a great likeness in the typical structure of his limbs to the *Anoplotherium*, we may infer that the fathers of both reduced forms bore also a general likeness; and this gives us a clue to the skeletons of the ancestors of the *Anoplotheridæ*, which is still further strengthened by many other considerations, of which I speak more fully in my paper.

Whilst trying to gain a more complete knowledge of the skeleton of the extinct Paridigitata, I became convinced that we must make some change in our zoological classification of the Ungulata in order to admit the great quantity of genera which have no place in the present system. After the breaking up of the Pachydermata (a name that has long enough obstructed science and really checked progress by holding together the most heterogeneous assemblage of animal forms), all the Paridigitata came to be divided into Suina and Ruminantia. This introduction of a physiological function into a system based on the struc-

ture of the skeleton is objectionable in the highest degree; besides, in this classification there is no room for those fossil genera which are certainly not Suina, and most probably did not ruminate. The greater the number of such genera, the better their organization and history are known, the more pressing the necessity to give them some adequate place in our zoological system. As an instance that such a necessity is keenly felt, we may cite Professor Leidy, who, in describing the *Oreodontidæ*, *Agriochœridæ*, &c. of Nebraska, says that they were "ruminating hogs;" but in reality they were not hogs at all, and most probably did not ruminate; what is, then, to be done with them?

The introduction of Professor Owen's* strict division between Paridigitata and Imparidigitata was a great gain to science; it radically separated two groups that previously were always hopelessly mixed together; but now the same principle must be carried further. The separation of the two groups of *Paridigitata* and *Imparidigitata* took place in very ancient time, not nearer than the Cretaceous period, and the striking diversity exhibited by both groups from the lowest Eocene is a proof of their ancient separation. But one of the branches, the *Paridigitata*, in its turn, split very anciently again into two distinct groups, one with tubercular, the other with crescentic teeth. This occurred at nearest in the Lower Eocene, perhaps even in the Cretaceous period. These groups, once separated, kept entirely apart and followed different lines of descent, although the modifications which both undergo along the descending lines are parallel and analogous even to the greatest details. Following these two divergent lines of descent, both groups culminate in the recent fauna in such forms as the *Phacochœrus* and *Dicotyles* for one group, and the *Bovidæ* for the other.



Links between them we discover none; and to discover their parentage, we must pass along the ascending lines to the point at which they diverge, as the linking genera, which doubtless existed at the time of separation, are long ago extinct, and both groups are now widely separated. I suggested this view, whilst studying in the British Museum the remains of *Hyopotamidæ*, to Professor Owen, and he finds no objection to it. He aided me

* Proposed before him by French anatomists, but never carried out completely.

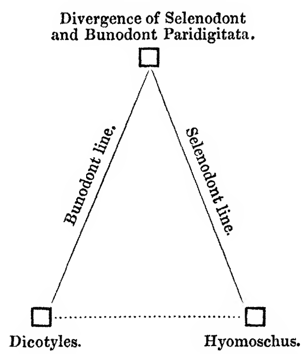
in finding for the two groups convenient names; and by his suggestion I should call the Paridigitata with crescentic teeth *Par. selenodonta*, and those with tubercular teeth *Par. bunodonta.*

To the *first* group would belong all the ancient and living Paridigitata having crescentic teeth, as the *Anoplotherium*, *Xiphodon*, *Dichobune*, *Anthracotherium*, *Bothriodon*, *Hyopotamus*, *Rhagatherium*, and the living Ruminantia.

The *second* would embrace all the Suina, Hippopotamina, and *Entelodon.*

Each one of these two groups may be again subdivided on the principles adopted in this paper.

By such division, we shall gain the advantage of having the Paridigitata arranged into two distinct lines of descent; every new discovered form will at once have its place along one of the lines, and the true pedigree of both will be ascertained much sooner and with greater accuracy. Whilst now making no such clear division, palæontologists, in projecting their genealogical tables, mix both groups together; and, according to the need of the moment, they place forms belonging to one line of descent in the other, and *vice versâ.* Thus, for instance, all the Hyopotamoids and *Anthracotherium* are constantly moved about from one line to the other *, while their true place is along the line of Selenodont Paridigitata; and they have nothing to do with the Bunodont Suina, although groups quite parallel with them may be found on the descending line of Bunodont Paridigitata. Such parallelism, however, does not imply direct links



along parallels drawn across both diverging and descending lines; the links are to be found only by climbing along the ascending lines to near the point of separation. For instance, *Dicotyles* and *Hyomoschus* occupy analogous positions; but there is no link between them along the dotted parallel. Links will be found only by going up to the point near their separation.

There are, no doubt, to be found around the points of divergence many forms of which it is difficult to say whether their teeth are tubercular or

* In fact described constantly as Suina. See Gervais, 'Paléontologie de France.'

crescentic, so thick are the lobes; but once this uncertain stage is passed, both groups keep unmistakably distinct.

Having once become convinced that these two groups of crescent-toothed and tubercular-toothed Paridigitata, after branching off from a common progenitor in the early Eocene (perhaps the Cretaceous) period, followed diverging lines of descent, never mixing together, I tried to ascertain accurately, by such data as were furnished by fossil remains and by lawful induction, what are the exact modifications of the skeleton exhibited by each group along the ascending and descending lines. As these modifications were most clearly given by greater or less reduction of the manus and pes, I subjected these to a detailed comparison.

In tracing the Paridigitata in time, we cannot mistake the tendency clearly manifested by them to a gradual reduction of the manus and pes in such a way that each descendant is always somewhat more reduced than its immediate predecessor. The limbs in the Ungulata serving only for the support of the body, and not for prehension, the organism seems to derive a great advantage from their reduction and simplification.

By a comparative study of the least reduced representatives on both lines, I tried to ascertain the probable structure of the manus and pes in the progenitor that has given rise to both groups, or to the whole assemblage of Ungulata; and this led me to construct a typical manus and pes. On the correctness of this scheme we may to a certain extent rely, as it is exhibited in nearly all its details by the living *Hippopotamus*, the most complete form of the living, and by the *Hyopotamus* and *Anthracotherium*, the most complete of the extinct, Paridigitata. Though such typical foot may be supposed to have been pentadactyle, still, as not a single living or fossil form has ever shown a trace or a rudiment * of the first digit (still less this first digit in a developed state), I thought it more convenient to adhere to facts, and give the foot as it is found in the most complete types, the first digit being always lost, and its carpal and tarsal bone helping to support the second digit. This fundamental typical structure of the manus and pes may be stated, in a few words, to be as follows:—

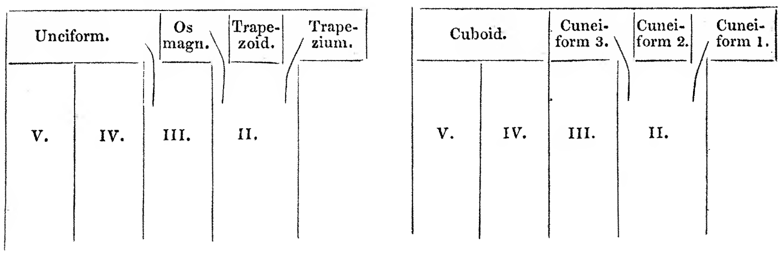
Supposing the foot to be pentadactyle, the two outer digits (the fourth and fifth) are always supported in the manus and pes by one single bone —the unciform in the manus, the cuboid in the pes; the three succeeding inner digits are supported each by a separate bone—the third, second, and first cuneiform in the pes, and the os magnum, trapezoideum, and trapezium in the manus. Besides, in the manus, the *third* digit, being supported by the magnum, also touches the unciform by a small ulnar projection, and the *second*, supported by the trapezoides, goes to touch the

* Prof. Huxley noticed this absence of rudiments of the first digit in his Anniversary Address of 1870 (Quart. Journ. Geol. Soc.). Such rudiments of the first digit, described in many cases, have proved always, on examination, to have been mistaken, the trapezium or the first cuneiform being taken as the rudiment of the first digit.

os magnum; the second digit of the pes is supported by the second cuneiform, and by its fibular projection is connected with the third cuneiform. The first digit is lost in all Ungulata, and its typical bone, the trapezium, or first cuneiform, helps to support the second digit.

Diagram of a Typical Foot in Ungulata Paridigitata.

Manus. Pes.



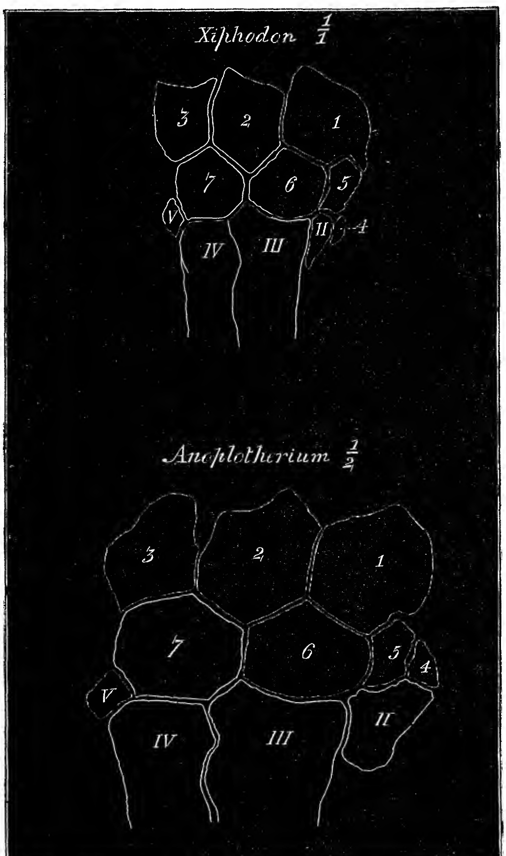
Beginning from this typical structure of the manus and pes, which was probably exhibited by the progenitors of the Paridigitata, we may follow its gradual reduction along both lines of descent in the crescent-toothed (Selenodont) and tubercular-toothed (Bunodont) Paridigitata. Both lines present a series of parallel modifications, and the parallelism is often carried to the minutest details. The only difference is, that along the crescent-toothed line (*Selenodonta*) the reduction is proceeding at a much quicker rate than along the tubercular-toothed (*Bunodonta*). The reason of this may consist perhaps in the commencing faculty of rumination in the former group, which faculty gave it an immense advantage over the latter. For the comparative anatomist this slow rate of change in the Suina is exceedingly welcome, as it brings the modification of the Suilline foot to our own time, and allows us to discover all the intermediate stages of modification, which, being passed over very rapidly, and in ancient periods, by the crescent-toothed group, have left none or but few traces of their existence.

By the reduction of the foot in Paridigitata, I simply mean that the function of locomotion which has been performed primitively by all the four (or five) digits begins to be carried on chiefly by the middle two, the lateral digits undergoing a gradual decrease. This, as I have said before, seems to be of great advantage to the organism, and is manifested by all descending lines of Ungulata.

In trying to ascertain the exact method of this reduction and its final results in recent and fossil genera, we come to very interesting facts that have not been duly noticed before, and which furnish us with the explanation of the presence of so many very reduced forms even in old Eocene and Miocene deposits. In both groups, the crescent-toothed (*Selenodonta*) and the tubercular-toothed Paridigitata (*Bunodonta*), we meet with a *two-*

fold mode of reduction of the manus and pes,—a simple or *inadaptive*, and an elaborate or *adaptive* mode.

Following the first or *inadaptive* mode of reduction, the foot, whilst losing its lateral digits, acquires no better adaptation to altered conditions of locomotion and support of the body than that which is derived from the mere thickening of the remaining digits. The relation between the carpal and tarsal bones and the remaining two middle metacarpals and metatarsals remains just the same as it was in the tetradactyle ancestor. The remaining digits do not exhibit any modification by which they receive more ample support from the carpal and tarsal bones, by taking the place formerly occupied by the now reduced and lost lateral digits. This mode of reduction I call *inadaptive*, or reduction in which *inheritance is stronger than modification*. As an instance of this inadaptive mode of reduction, I may point out the foot of *Anoplotherium* and *Xiphodon*. The annexed diagram clearly illustrates



this mode of reduction. The fourth digit does not even take the whole of the unciform, and a part of this bone is still occupied by the useless rudiment of the fifth digit; the third has not extended over the whole os magnum; and the useless rudiment of the second digit occupies its typical place on the trapezoid, touching the os magnum, and being additionally supported by the trapezium.

Following the second or *adaptive* mode of reduction, the middle digits grow larger and thicker than in the first mode; but whilst broadening transversally they do not adhere to the ancestral pattern, but tend to gain a better support on *all* the bones of the carpus and tarsus; they deviate from the ancestral type, push the lateral digits (while these are yet completely developed) to the side, and usurp their typical carpal and tarsal bones for their (the middle digits) own use, thus gaining a better and more complete support for the body. The lateral digits, deprived of their typical carpal and tarsal bones, and taking henceforth no active part in locomotion, tend to disappear; and every millimetre that is lost by the lateral digits is immediately taken possession of by the enlarged middle ones; so that even before the entire disappearance of the lateral digits the two middle digits have usurped the whole of the distal surface of the carpus and tarsus, the fourth digit has spread over the whole unciform (manus) and cuboid (pes), and the third has taken possession of the trapezoid (manus) and second cuneiform (pes). This once attained, the two middle digits, being pressed from both sides by the carpal and tarsal bones, begin to coalesce, forming the so-called *cannon* of the recent Ruminantia, or of the hind foot of *Dicotyles*. This mode of reduction I call the *adaptive*, or reduction in which such *modification keeps pace with inheritance*.

As an instance of this mode, I may cite the foot of *Sus*, *Dicotyles*, *Hyomoschus*, Ruminantia. Every anatomist will acknowledge that this second mode of reduction is much more useful to the organism than the first.

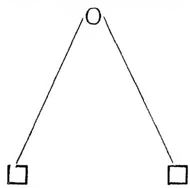
If we inquire further what are the genera which follow the first or *inadaptive* mode of reduction, we find that *all extinct* genera of Paridigitata follow it, while all *living* * genera follow the second or adaptive mode of reduction.

This being the state of the case, the questions arise, Did they not become *extinct* because of their incapacity to adapt themselves completely to altered circumstances? and did not the others *survive* because they adapted themselves more fully to these circumstances? I will try to consider both cases in reference to the living and fossil Paridigitata.

I said before that early in the Eocene period the group of Paridigitata split dichotomously into two secondary groups, one with crescentic teeth, the other with tubercular; the first I have called the Selenodonta, the second Bunodonta (or Suina). Now each of these secondary groups fol-

* Or fossil forms which continue to live, or have left direct successors, as *Palæochœrus* and the Miocene Ruminantia from Auvergne.

Early Eocene Paridigitata.



Tubercular-toothed Paridigitata. Crescentic-toothed Paridigitata.

lowed a twofold mode of descent, one of which I term the *inadaptive*, and the other the *adaptive*, thus, finally, giving rise to four distinct groups:—

Paridigitata with crescentic teeth (Selenodonta).

A. The group following the *inadaptive* reductions develop enormously in Eocene and Middle Miocene times: all have distinct metacarpalia and metatarsalia, five-lobed upper molars, smooth distal extremities of the metapodials. Genera: *Bothriodon*, *Dichobune*, *Rhagatherium*, *Cainotherium*. They reached their highest development and culminated in the didactyle *Anoplotherium*, *Xiphodon*, and *Diplopus*, which all became extinct without direct successors.

B. The group following the *adaptive* reduction separated from the group A somewhere in the Middle Eocene, by some of the small *Hyopotamidæ* acquiring four-lobed upper molars, as met with at Mauremont, and becoming *Dichodons*. Intermediate stages little known; the *Gelacus* is one of them. The least reduced living form is *Hyomoschus*. Culminating in recent times in the didactyle *Bovidæ* and *Antilopidæ*.

Paridigitata with tubercular teeth (Bunodonta or Suina).

A. Group following the *inadaptive* reduction very little known. *Acotherulum* and another larger hog-like animal from the Middle and Upper Eocene may belong to this group; they were certainly tetradactyle. Culminated in the lowest Miocene in the didactyle *Entelodon*: no successors.

B. Group following the *adaptive* reduction, branched from the group A in the Eocene; the most typical representative is the *Chœrotherium* from Sansans, with the phalangeal ridge not yet extending over the whole distal end of the metapodium. *Palæochœrus*: reduction has fairly set in on the adaptive mode, the phalangeal ridge passing over the whole end of metapodial. *Sus* still more reduced. *Dicotyles*: *all* the distal surface of the carpus and tarsus taken by the enlarged middle digits. Tending to become *didactyle*.

We must briefly consider each of these groups.

The Paridigitata with crescentic teeth following the *inadaptive* mode of reduction, and whose skeletons are known, are the *Anoplotherium*, *Xiphodon*, *Anthracotheridæ*, and *Hyopotamidæ*. If it should be asked *why* they followed this mode of reduction, the reason is obvious. Admitting that an advantage is gained by the simplification of the foot and the reduction of the number of digits, this mode of reduction is the most simple course to be taken. We must imagine the enlargement of the middle digits to be accompanied by a broadening of their correspondent bones in the carpus and tarsus; the trapezoideum and the second cuneiform were simply pushed aside (not made use of) by the enlargement of the third digit, and their reduction kept pace with the reduction of the second digit. If we think how the process must have gone on "*in naturâ*," we shall find that it required quite an unusual occurrence, some happy chance, for the third digit to go over the separating line between the magnum and trapezoideum, or the third and second cuneiform, and get a footing on these last bones, which typically belonged to the second digits. This was evidently the most advantageous mode, but it did not occur at once; and the organism has taken the more simple and obvious inadaptive mode, which, once fairly set in, could not be changed. This branch of the Paridigitata then, starting from their tetra- (or penta-)dactyle progenitors in the Cretaceous or earliest Eocene, arrived at the close of the Eocene (from which strata alone we have Paridigitata whose skeletons are known) to the reduced didactyle forms, known as the *Anoplotherium* and *Xiphodon*. That these last had tetradactyle ancestors is supposed, on theoretical grounds, by the evolutionists; besides, their rudimental second and fifth digits point clearly to some form in which these rudiments were completely developed and used for locomotion.

Whilst trying to ascertain the structure of the skeleton of an extinct family (*Hyopotamidæ*) allied to the *Anoplotheridæ*, but which was supposed to be chiefly Miocene, I found that the Miocene genera could be regarded only as the last representatives of this exceedingly numerous family, whose chief development fell in the Eocene times, when it was represented by numerous subgeneric and even generic forms. I was fortunate enough to find, in the collection of M. Aymard, at Puy, a large assemblage of bones belonging to the oldest Miocene representative of this family, the *Hyopotamus*; indeed so much, that I could completely restore the limbs and nearly the whole skeleton. The limbs prove to be tetradactyle, with well-developed lateral digits. The same family is so richly developed in the Eocene, that we have a full right to suppose that the older genera had even a more completely developed manus and pes.

From Puy I came to London to complete my study, as teeth which were not to be distinguished from the *Hyopotamus* of Puy were known to be numerous in England; and whilst studying the bones found in England, I was struck by the fact that some of these belonged to a didactyle genus

of the same family, which in England proved to be associated with the tetradactyle genus. To this new genus of the Hyopotamoid family I gave the name *Diplopus*. This was indeed a welcome discovery—ancestor and descendant existing together, the complete with the reduced form living about the same period*. Moreover, the didactyle form bore a great general likeness in the structure of the limbs to *Anoplotherium* and *Xiphodon*, being perhaps only a little more elaborate and better adapted than these first experiments of the Eocene times.

The likeness of the descendants allowed me to make inferences as to the likeness of the ancestors; and, taking into consideration the structure of the limbs in the tetradactyle *Hyopotamus*, and the rudimental second and fifth digit still existing in *Anoplotherium*, *Xiphodon*, and *Hyopotamus*, I feel confident that the supposed ancestor of the first two did really possess a *manus* and *pes* very like the projected typical diagram; indeed we may be nearly as confident of this as if we had found the actual thing imbedded complete in some early Eocene or even Cretaceous rock.

This, then, was the state of things in the earliest Eocene; large numbers of Paridigitata with tetradactyle feet like our *Hyopotamus*, and the supposed progenitors of *Anoplotherium* and *Xiphodon*, represented the group of Paridigitates with crescentic teeth (*Selenodonta*). Reduction in the number of digits, being an advantage to the organism, was steadily going on. But, be it observed, we follow now the *inadaptive* line of descent; and while the whole weight of the body was, by gradual steps, entirely transferred to the two middle digits, these thickened and grew larger, but entered into no special adaptation by means of which they should better perform the work which had fallen to their share; they did not enlarge so as to gain additional support from all bones of the second row of the carpus and tarsus; the reduction was inadaptive: inheritance is in them stronger than modification.

Seeing that old Paridigitata present only two free metacarpals and metatarsals, and that recent Ruminantia have the same two metacarpals and metatarsals coalesced into a single cannonbone, evolutionists generally rush at the seemingly obvious conclusion that once the tetradactyle foot reached the reduced state of two digits, these coalesced together, and were transformed into the cannonbone of Ruminants. No such thing, however, happened; nor could it have happened with the old didactyle Paridigitata, as the *Anoplotherium*, *Xiphodon*, and *Diplopus*; and the reason why it could not is clearly indicated by the structure of their feet. We have already shown that, following this *inadaptive reduction*, the two middle digits, whilst growing larger, continue to occupy only the inner half or more of the unciform and the greater part of the os magnum; so that from the outer as well as from the inner side the carpal bones which support useless rudiments overhang the two middle functional digits. In con-

* Such cases are numerous. In the Sewalik Hills the *Hipparion* is associated with the horse.

sequence of this, the distal surface of the carpus was much broader than the proximal surface of the two functional digits—an arrangement not calculated for firm equilibrium. Now the confluence of the two middle digits is always followed by a considerable contraction; and if this coalescence should occur in the imperfectly adapted foot of *Anoplotherium*, and especially *Xiphodon*, all equilibrium would be lost. If ever such confluence occurred, by reason of the tendency to the greatest possible reduction, the resulting form had not the least chance of being propagated and of holding its ground against the competing genera. The broadening of the middle digits could not occur after the entire loss of the laterals; and we shall see that, in genera which have left immediate successors (*Sus*, *Hyomoschus*), the lateral digits are not allowed to go until the middle ones have obtained a secure footing on the entire distal surface of the carpus and tarsus. However, these inadaptively reduced genera of the Eocene could perhaps have lived till our own days; but the development of the competing and better adapted forms pressing them on all sides, they had no chance to stand their ground against them, and became extinct without any direct posterity, while the succession of the Paridigitata Selenodonta was carried by a side branch, and reached its culminating point in the Miocene, continuing from thence to our own days.

We turn now to the same mode of *inadaptive* reduction as manifested by the tubercular-toothed Paridigitata (*Bunodonta*), or Suina. The old representatives of this group are very little known. The *Chœropotamus* is a very doubtful genus, and may be inclining towards the crescentic-toothed Paridigitata, being supposed to be the progenitor of the *Anthracotheridæ* and *Hyopotamidæ*. Besides it we have the *Acotherulum saturninum*, Ger., a truly tubercular-toothed Paridigitate from the Upper Eocene, *Acotherulum Campichii* (*Dichobune*, Camp. Pictet) from the *Lower Eocene* of Mauremont, and a larger pig-like animal from the same deposit not yet described or named. These are undoubtedly the oldest tubercular-toothed Paridigitates we know; but unfortunately our knowledge is based only on dental characters. However, considering that even the recent Suina have not yet completely lost their two lateral digits, it may, with the greatest probability, be inferred that these old Eocene forms were tetradactyle. Our knowledge of the development of this group is very incomplete; but there can be no doubt that, though not nearly so rich as the Selenodont group, they were still numerous, as may be inferred from the great quantity of the Suina in the Miocene, and such forms as the *Listriodon splendens* *. We are so accustomed to look on the Suina as a group of tubercular-toothed *tetradactyle* Paridigitata, that no one ever thought of the possibility of a *didactyle* hog; but, strange as it may seem, such a Suilline animal

* I have not been so fortunate as to see any bones of the *Listriodon*; but as this miocene hog died without any successors, I should not be astonished if it proves to be didactyle, thus being a parallel to *Hyopotamus* in the same sense as *Entelodon* is parallel to *Anoplotherium*.

existed; stranger still, it existed in such an ancient period as the close of the Eocene in the lowest strata of Ronzon at Puy. This is the *Entelodon*, Aym. (*Elotherium*, Pom., *Archæotherium*, Leidy). The Suilline characters are so striking in this form, that it was at once placed among the Suina, and pronounced tetradactyle, though the confluent tibia and fibula (mentioned by Leidy) might have been taken as a warning against rash conclusions. I have found in the cabinet of M. Aymard, in Puy, some bones of this animal; few it must be acknowledged, but still leaving no doubt as to the didactyly of *Entelodon*. Of this I shall try to adduce more extensive proofs in a forthcoming memoir on this genus. How can the presence of a hog with such reduced limbs be explained in such ancient deposits, when even the living *Suidæ* have not yet reached this stage of reduction? The fact, however, is intelligible when we consider that the *Entelodon* is the final result of the *inadaptive development* and reduction along the line of tubercular-toothed Paridigitata; it is the *culmination point* of this group, and in this sense quite parallel to the *Anoplotherium* in the other group. Thus the Paridigitata, which split dichotomously in the earliest Eocene (?) into two groups, the tubercular-toothed (*Bunodonta*) and the crescent-toothed (*Selenodonta*), following the inadaptive mode of reduction, reached their culmination point in the Upper Eocene or just above it, in such forms as *Entelodon* for the first group, and *Anoplotherium*, *Xiphodon*, *Hyopotamus* for the second group, which all became extinct without any direct posterity. The living Suina and Ruminantia are not directly connected with them, but are the issue of lateral branches which followed the adaptive mode of development and reduction.

We may now consider the results of the *adaptive* mode of reduction. As I said before, the rate of this reduction is much slower in the tubercular-toothed Paridigitata, or Suina; and this gives us the means of following more closely all the stages of reduction. I propose, therefore, in the first place, to consider these.

Though the published materials, as far as the skeleton is concerned, are very poor, we have the means of giving nearly all the intermediate stages between those genera in which the manus and pes are conformable to the true tetradactyle type, every digit (except the fourth and fifth, which are always borne by one) being carried by a separate carpal and tarsal bone, and those in which the entire distal surface of the carpus or tarsus is taken by the enlarged two middle digits.

The adaptation of these two middle digits on the adaptive line forms a striking contrast to their rigidity exhibited by the other mode of reduction; and we shall briefly indicate the stages by which the typical Suilline foot actually passed to reach the stage exhibited now by *Dicotyles*.

We are at a total loss to indicate the precise time when the adaptive branch separated from the inadaptive; it was certainly somewhere in the lowest Miocene, as in the Middle Miocene we find already a large quantity of Suinæ in which the adaptative reduction has fairly set in. As the first

stage I must consider a small Suilline animal, though not the oldest, but perhaps a remnant of the older type; this is the *Chœrotherium*, Lart., from Sansans. The primitiveness of this small pig is indicated by the fact that the carpal and tarsal bones retain their typical relation to the four metacarpals and metatarsals; the humerus is very *Anoplotherium*-like, and the distal extremity of the metapodium is smooth anteriorly, the phalangeal articular ridge being limited only to the palmar side, as in all ancient Paridigitata.

First Stage, *Chœrotherium*, Lart., Sansans.—The middle digits are enlarged, but the laterals still retain their typical relation to the supporting bones of the carpus and tarsus*. Distal end of humerus *Anoplotherium*-like (ancient); the proximal end of the radius, in correspondence with the humerus, is also *Anoplotherium*-like. The distal end of metapodium is smooth, the phalangeal ridge being limited to the palmar side.

Second Stage, *Palæochœrus* (Allier).—The adaptive reduction of the *manus* and *pes* has fairly set in, its first indication being that the radial margin of the third digit (in the manus and pes) is raised in such a way as to exclude the second digit from going to its typical facet on the os magnum and third cuneiform, though leaving it still in the full possession of the trapezoid and second cuneiform. The phalangeal articular ridge is passing from the palmar side round the distal extremity to the anterior face of the metapodium.

Third Stage, *Suidæ*.—Adaptive reduction is proceeding further, the middle digits are greatly enlarged, and the third digits of the manus and pes spread over one half the trapezoideum and nearly the whole of the second cuneiform. The lateral digits touch the ground only very slightly, and are not important for locomotion.

Fourth Stage, *Dicotyles*.—The middle digits are so enlarged and adapted that the entire distal surface of the carpus and tarsus is taken by them; the lateral digits have no distinct facets on the distal surface of the carpus, and are merely hanging to the enlarged middle digits. The fifth digit of the pes is lost, and the two metatarsals are coalesced into a cannonbone; the metacarpals are also so closely pressed together that their confluence is imminent. The complication of the stomach, which is divided into three chambers, shows a beginning of rumination, slight traces of which are even exhibited by the common hog; the premolars become complicated, and begin to assume the shape of molars†, the first premolar is lost (as in all Ruminants), the incisors reduced to four, the canines are small.

Fifth Stage.—The culminating point is not yet reached by the tubercular-

* That is, the second digit is supported by the trapezoideum, and has besides a facet on the os magnum, as in *Hippopotamus*, or in the typical tetradactyle foot generally.

† A very important circumstance, considering that we meet the same fact in other groups where the premolars assume the shape of molars, as in *Palæotheridæ*, horses rhinoceros, &c.

toothed Paridigitata, following the adaptive mode of reduction; but as it was reached by the same group on the *inadaptive* mode (*Entelodon*), and as the parallel group of crescent-toothed Paridigitata, whose reduction is going at a quicker rate, has already reached it, there can be no doubt that the Suina are tending also to the same culminating point. In reaching it the lateral digits will be entirely lost, the trapezium will coalesce with the magnum, and the second cuneiform with the third; the middle metacarpals and metatarsals will coalesce into a complete cannonbone, and probably the stomach will become still more complicated, and they will ruminate. That this state is the goal towards which the Suina tend I have little doubt; but it is more than probable that man by his influence will prevent them from ever reaching it.

Our task is more difficult when we come to inquire into the line of descent which has given rise to the Ruminantia. As stated before, I cannot put the *Anoplotherium*, nor the *Xiphodon*, in their pedigree. In my opinion, the line which ends in Ruminantia branched off from the small tetradactyle *Hyopotamidæ*, which were so numerous in the Eocene period. I find in the Eocene of Mauremont all stages of transition between the *five-lobed upper molars* of these Hyopotamidæ and teeth having a true ruminant four-lobed pattern; these last have belonged to some small species of *Dichodon*. Unfortunately we have no clue to the skeleton, though, seeing the tetradactyle living *Hyomoschus*, it may fairly be assumed that these early progenitors of Ruminantia were also tetradactyle. The small tetradactyle *Cainotherium* is a very tempting genus in speculations about the descent of Ruminantia; but I must exclude it for many reasons, though I cannot here give them in full. Some of these are as follows:—the *Cainotherium* retained till the Middle Miocene five-lobed teeth on the *Dichobune* pattern (with the three lobes on the posterior half of the tooth), while we have truly ruminant teeth already in the Eocene; it retained its upper incisors and free metatarsals, while the much older *Gelacus*, Aym., which is already a true ruminant, had no upper incisors and the metapodials were confluent in the adult. *Cainotherium* seems to be a direct descendant of *Dichobune*, and to have become extinct, without leaving any successors.

Supposing that the *Dichodon* had a foot true to the tetradactyle type, we do not find the earliest stages of reduction; they were passed rapidly, and in very ancient times: but there can be little doubt that the Ruminantia began with a tetradactyle foot, and ended by a cannonbone adapted to the whole distal surface of the carpus and tarsus. Such adaptation of the two middle digits could not be obtained at one leap; and certainly all stages between a tetradactyle foot (in which every digit was supported by a separate bone in the carpus and tarsus) and a didactyle foot (in which the two enlarged middle digits have taken the whole distal surface of all the carpal and tarsal bones) were passed by this group in the same manner we have seen it in the Suina, but only a

few traces of this passage remain. From the tetradactyle *Dichodon*, the group of adaptive Selenodonts may be said to have split in two subordinate groups. In one of these, represented by the *Hyomoschus*, the lateral digits are retained, and only the metatarsals become confluent, while the two middle metacarpals continue to be free*. In the *Tragulidæ* the two middle digits coalesce, in both fore and hind limbs, into a complete cannonbone, but the lateral digits are still retained in their whole length as useless, nearly filiform appendages. The distal surface of the metapodium remains smooth; the rumination is incomplete.

In the other group, as the representative of which we may cite the *Gelocus*, Aym., the lateral digits were soon lost, and the remaining two middle digits have taken the entire distal surface of the carpus and tarsus; still they remain separate, perhaps through life, in some of the Eocene *Geloci* whose remains I have seen from the phosphatic limestone deposits in the south of France, near Cahors, in a locality called Caylux. In this deposit the bones of *Gelocus* are found, together with large *Anoplotheria* and *Palæotheria*, and even the completely ossified and not epiphysed metatarsals are found entirely free. In the lowest Miocene of Puy, however, we find a *Gelocus* whose metacarpals and metatarsals are free only in the young, and coalesce in the adult; but, even after their coalescence, the distal end of the metapodium is smooth, and the articular ridge is limited to the palmar side. In the somewhat newer (about the upper part of the Lower Miocene) deposits of Allier, in Auvergne, we meet at last with metatarsals and metacarpals entirely coalesced into a complete cannonbone, and the articular ridge taking the whole distal extremity of the metapodium. Small rudiments of the lateral digits (second and fifth) still remain as styliform appendages on both sides of the cannonbone, in the fore and hind limbs.

Such true ruminant forms are exceedingly numerous in the Miocene of Allier; they are all hornless, and some retain seven molars in the lower jaw, as in all ancient Selenodonts. In most, however, of these newer Miocene forms the first premolar of the lower jaw is lost, and they exhibit the same dental formula as the living Ruminantia, from which they seem not to differ in any of the essential characters. These true ruminant forms of the Lower Miocene may be considered to have reached the culmination point of their reduction, and we shall consider them as such. Thus the Selenodont Paridigitata, after branching off from the common stock in the Lower Eocene, reach the utmost stage of reduction on the adaptive mode a little below the Middle Miocene; this we consider to be the fifth stage, or the culmination.

The fifth stage, or the culmination point of the Paridigitata Selenodonta,

* These middle metacarpals and metatarsals are enlarged and adapted to the whole distal surface of the carpus and tarsus.

following the adaptive mode of reduction, means that the reduction of the manus and pes was carried so far that it could not proceed further; this point was attained already in the Lower Miocene. When once the metapodium was reduced to *one* bone, and this one had taken the whole distal surface of the carpus and tarsus, any further reduction or improvement was quite impossible. Besides, the completely developed faculty of rumination gave these forms an enormous advantage over the other, non-ruminant, Paridigitata occurring in the same strata. They could live on such matters as twigs, bark of trees, mosses, lichens, on which no other Ungulata can subsist; such food is found everywhere, requires no cunning and very little struggle to get it. All essential modifications were attained very early, and the chief of these are the confluence of the two middle digits in a complete cannonbone and rumination. Then began the luxury of all sorts of appendages—excrescences on the frontal bones covered with skin, uncovered by skin in the form of prickly simple horns (*Pudu*), or double (*Dicroceras* of Sansan, Muntjac), then branched and palmated. In other groups these bony cores were covered with horny sheaths, which at first differed but little from agglutinated hairs (*Antilocapra americana*), then became more compact, as in the smooth and hard horny sheath of the hollow-horned Ruminantia. These secondary characters were all acquired, thanks to abundant time, after the essential characters of the type had been assumed; if man had come on earth a little later than he did, he certainly would have found nearly parallel cases in the group of Suina, monodactyle (with cannonbone) hogs with different appendages. As it is, he stopped the course of events; all further improvement is out of the question, or only possible in such groups as the Rodentia, who prey on man's food, being at the same time independent of him.

It may be asked, How stands the matter in the Imparidigitate Ungulata? And though I cannot enter fully into the case, I may state that the same course of events is observable in them; only there could be no *inadaptive* reduction, as the body could not, under any circumstances, be held in equilibrium upon one single third digit, if this one had not taken the whole distal surface of the carpus and tarsus. But the task in this group was much more difficult; to get one middle digit to perform the work shared in the ancestors by five, and in the immediate progenitor by three, required time. To accomplish this, two geological periods were needed; but still, by the incessant tendency to reduction, the work was done, and the monodactyle horse spread over the surface of the globe, superseding all other Imparidigitata, which are evidently rapidly dying out. The only *two* genera which remain still, the Rhinoceros and the Tapir, cannot last long. But this spreading and multiplication of the *Equidæ* was also accompanied by a total change of diet: from an omnivorous animal it became grass-eater; and indeed, by its teeth and many other characters, the horse is very *analogous* to the Ruminantia,

being, as they are, the culmination point of the group of Imparidigitata. The reduction of the horse foot, however, is not fully accomplished yet; to attain this, the styliform metatarsals and metacarpals (the second and fourth) have to be lost.

II. "Magnetic Survey of Belgium in 1871." By the Rev. S. J. Perry. Communicated by Sir Edward Sabine, K.C.B., F.R.S. Received January 24, 1873.

(Abstract.)

The magnetic observations which furnished the results contained in this paper were made during the autumn months of 1871.

The instruments used and the methods adopted were almost identical with those employed in previous magnetic surveys of France.

The dip was observed by Mr. W. Carlisle, magnetic assistant of Stonyhurst Observatory, and the rest of the observations were taken by the Rev. S. J. Perry.

This new series of determinations of the terrestrial magnetic elements was rendered the more necessary, as preceding observers had chosen very few stations in Belgium, and as the curvature of the isodynamics and isoclinals in Dr. Lamont's maps of Belgium, Holland, and North-west Germany indicated a very considerable disturbing cause in the first-named country.

The values obtained in 1871 are a strong confirmation of the suspicions of irregularity to which former observations had given rise; for although the lines of equal dip, declination, and horizontal force bear a sufficiently close resemblance to those of neighbouring countries, there is evidence of much disturbance; and when the values of the dip and horizontal force are combined, the isodynamics show clearly that the coal-measures, which stretch completely across the south-east portion of Belgium, exercise a strong disturbing influence. This local magnetism might be incapable of producing more than a decided curvature of the isodynamics of an extended tract of country; but when all the stations of observation are situated within narrow limits, the perturbation completely masks the normal direction of the lines.

The following is a complete list of the magnetic elements observed at the different stations, and reduced to the common epoch of January 1, 1872:—

Station.	Declination.	Dip.	Horizontal force.	Intensity.
Aix-la-Chapelle	16°·464	66°·637	4·0064	10·1025
Alost	17·349	67·210	3·9518	10·2016
Antwerp	17·489	66·999	3·9296	10·0559
Arlon	16·398	65·907	4·1175	10·0857
Bruges	17·938	67·155	3·8950	10·0321

Xiphodon $\frac{1}{1}$

Anoplotherium $\frac{1}{2}$